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THE ATLANTIC AMERICAN SPECIES OF THE FISH GENUS GASTEROSTEUS

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I

The systematic interpretation of the sticklebacks has long been—and still remains—one of the most perplexing problems in ichthyology. Because of this difficulty, the classification of these little fishes has been a confused vacillation. This condition is preëminently true of *Gasterosteus,* as that genus has generally been delimited in recent years.

The multitudinous forms of *Gasterosteus,* many of which have received scientific names, are with one notable exception all interconnected by intermediate types (see figures). Such general tendencies toward a regular geographical gradation of types as do exist are so inconspicuous as to be all but occluded by the geographically unorganized local raciation: adjacent races very unlike in their structural characters, for example, may each find their essential counterparts in far distant forms. So numerous are these local races, so confused their geographical distribution, that it seems unwise to recognize any one of them (with the exception already mentioned)

as a distinct species. I refer them all specifically to *Gasterosteus aculeatus* Linnaeus.

The real interrelationships of these races of three-spined sticklebacks cannot be determined without recourse to a prolonged and critical statistical analysis of scores of natural populations. Very probably breeding and transference experiments will also be required, especially to determine the extent to which the apparently racial characters may be modified by the direct action of the environment on the individual. Without question the needed investigation will be one of unusual magnitude and complexity; that, however, is a fascination and a challenge.

The purpose of the present paper is not to discuss these problems of the status of the members of the *aculeatus* form-series. It is rather to help clear the decks for such a discussion, (1) by emphasizing the distinctness of the one form of three-spined stickleback which cannot be aligned in that series, (2) by attempting to untangle the complicated systematic history with which it, like other sticklebacks, has become ensnarled, and thus (3) to indicate the proper name which it should bear. To anticipate this discussion, I will state now that the apparently valid name for this species, shown on Plate II, figure 3, is *Gladiunculus wheatlandi* (Putnam).

II

"*Gasterosteus*" *wheatlandi* differs from *Gasterosteus aculeatus* in these respects:

(1) The pelvic spine is armed on *each* side by a strong basal cusp, sharply differentiated from the minute denticulations along the side of the spine. This character has been pointed out by most authors, and is illustrated anew on Plate II, figure 3a.

(2) The pelvic fin has two soft-rays (rarely one on one side) instead of only one, or sometimes none. This feature has been consistently overlooked, except by Jordan and Hubbs.[1]

[1] Mem. Carn. Mus., 10, 1925: 202, footnote.

(3) The dorsal and anal soft-rays are usually fewer.

(4) The colors are different.

(5) The body is always unarmed by bony plates on the posterior part (in one known specimen, as noted by Kendall, small plates are developed posteriorly), and the caudal peduncle is never keeled, and is more compressed than in *aculeatus*. The truly marine forms of that species are completely armored, and have the caudal peduncle dilated into a sharp keel on each side; only the extreme fresh-water types, like *Gasterosteus aculeatus williamsoni* (Plate II, figure 2), have no caudal keel.

(6) The habitat of *wheatlandi* is almost strictly marine; it often leads a semipelagic existence, especially near floating algae; it is true that it does penetrate to some extent into bays and saline sloughs (except near the southern end of its range), but it apparently does not wander into the fresh tidal waters. *Gasterosteus aculeatus*, in contrast, abounds in brackish and fresh tidal waters (with or without structural modification) and penetrates the coastwise streams for many miles, in some instances for hundreds of miles. Sometimes, of course, the habitats of the two species do overlap.

(7) The range of *wheatlandi* is much more limited than that of *aculeatus*—instead of being circum-subarctic, it is confined to the coastal waters from Newfoundland to southern Massachusetts.

So striking are these differences, especially the two first listed, that I recommend the generic separation of *wheatlandi* from *aculeatus*. For the genus, the name *Gladiunculus*, recently based by Jordan and Evermann[2] on "*Gasterosteus gladiunculus* Kendall = *G. bispinosus* Walbaum, fide Kendall," is available.

III

So far as I can discover, *Gladiunculus wheatlandi* was first described by Cuvier and Valenciennes,[3] from Newfoundland, under the name is "*Gasterosteus biaculeatus*, Penn., Sh. et

[2] Proc. Calif. Acad. Sci. (4), 16, 1927: 504.

[3] Hist. Nat. Poiss., 4, 1829: 368 or 503 (different editions).

Mitch." Their statements that this form has an unarmed caudal peduncle, and that it is distinguished from the other species by having a large, flat and pointed tooth on each side of the pelvic spine, clearly show that they had at hand an example of the species of stickleback which we have under consideration. That this is indeed the case is confirmed by the redescription and figure of Cuvier and Valenciennes' types, presented by Sauvage.[4]

The next original description of the species was, seemingly, that of Putnam,[5] who named it, in connection with a clearly recognizable account, *Gasterosteus wheatlandi* (type-locality—Nahant, Massachusetts). Goode and Bean[6] uncritically referred *wheatlandi* to the synonymy of the wholly armed type "*trachurus*" of *Gasterosteus aculeatus*. Storer,[7] however, accepted the species as valid, and used Putnam's name for it.

Eigenmann, in his revision of the American Gasterosteidae, introduced additional confusion to the case, already considerably involved. His "*Gasterosteus wheatlandi,*"[8] claimed to be from the coast of Massachusetts, is clearly not an Atlantic American stickleback; one of his described specimens is shown as Figure 2 of Plate II. There can scarcely be a doubt that this is an example of the southern Californian subspecies of *Gasterosteus aculeatus,* namely *G. a. williamsoni* Girard. In any case the figure is an adequate representation of that form, which is one of the most extreme southern fresh-water derivatives of the *aculeatus* series, independently convergent toward *G. wheatlandi* in the lack of a caudal keel, and still more degenerate in lateral armature (often lacking all the plates), but showing the ventral fin structure of the *aculeatus* group, and connected with typical *aculeatus* through an intergrading race in Santa Clara River, just northward of its range, and thence

[4] Nouv. Arch. Mus. Hist. Nat. Paris, 10, 1874: 21, pl. 1, fig. 12.

[5] Proc. Essex Inst., 5, 1867: 4 (also in Storer, Mem. Amer. Acad. Arts and Sci., 9, 1867: 279).

[6] Bull. Essex Inst., 11, 1879: 5.

[7] Mem. Amer. Acad. Arts and Sci., 9, 1867: 279.

[8] Proc. Acad. Nat. Sci. Phila., 1886: 241 and 246.

through *Gasterosteus aculeatus microcephalus,* which in turn merges into subspecies *aculeatus.* After having thus misidentified *G. wheatlandi,* Eigenmann confounded that species with *G. dimidiatus,* which is really a fresh-water race of *aculeatus* from Greenland.

G. wheatlandi was again named in 1896, when Kendall[9] described, as *Gasterosteus gladiunculus,* some specimens caught under floating algae near Seguin Island, off the coast of Maine. He accurately listed most of the main distinctive features of the species. I have examined the types of *gladiunculus,* and am convinced that they represent the same species as do the types of *wheatlandi,* which I have also studied.

Somewhat later, Kendall[10] recognized this identity of his *gladiunculus* with Putnam's *wheatlandi* and with Cuvier and Valenciennes' *biaculeatus.* He further assumed that this form was also identical with Shaw's *biaculeatus,* with Walbaum's *bispinosus* and with Pennant's and Foster's "two-spined stickleback." In order to accord this latter assumption the necessary test, we must pass these old accounts in brief review.

Forster,[11] in 1771, listed a stickleback, later shown to have come from the vicinity of New York, probably from Hempstead, Long Island, under the obviously erroneous name of "two-spined stickleback"; he must have overlooked the small spine at the front of the main dorsal fin. Forster gave no word of description whatever. And solely on his authority there were in succession based a series of strict *nomina nuda;* the "two-spined stickleback" of Pennant;[12] the *Gasterosteus*

[9] Proc. U. S. Nat. Mus., 18, 1895 (1896): 623 (also in Jordan and Evermann, Bull. U. S. Nat. Mus., 47, pt. 3, 1898: 2836). See also Smith, Bull. U. S. Fish Comm., 17, 1897 (1898): 93.

[10] Science, 15, 1902: 588; also Occ. Pap. Boston Soc. Nat. Hist., 7, 1908: 63. See also Sumner, Osburn and Cole, Bull. U. S. Bur. Fish., 31, 1911 (1913), pt. 2: 746; also Huntsman, Contr. Can. Biol., 1921 (1922), No. 3: 61, and Bigelow and Welsh, Bull. U. S. Bur. Fish., 40, 1924 (1925), pt. 1: 171.

[11] Catalogue of the Animals of North America, 1771 (reprinted by Willughby Society in 1882): 22.

[12] Arctic Zoology, 2, 1784: 385.

bispinosus of Walbaum[13] and the *Gasterosteus biaculeatus* of Shaw.[14] Shaw, to be sure, does give an apparent diagnosis—"*G. spinis dorsalibus duabus*"—which, however, was based solely on Forster's name, and is clearly erroneous as applied to any form of stickleback. Shaw's name *biaculeatus,* therefore, is as clearly a *nomen nudum* as is Walbaum's *bispinosus.* Either name, to attain validity, must, according to the accepted rules of nomenclature, rest on and date from the account of the first author to use the name in conjunction with a recognizable description, figure or other indication of identity.

So far as I know, Walbaum's name *bispinosus* was not resurrected until 1898, when Jordan and Evermann[15] applied it to the American marine type, which is almost identical with the typical *aculeatus* of Europe. They of course gave a recognizable description. Clearly, then, unless some earlier work now overlooked conflicts, the name *bispinosus* belongs with the *aculeatus* series and not with *wheatlandi.*

The first valid proposal of the name *biaculeatus* was, according to all available evidence, that of Mitchill.[16] In his early monograph on The Fishes of New-York he gave in 1814 a brief description of a New York stickleback under the name of *Gasterosteus biaculeatus.* His account follows:

> 1. *Two-spined Stickleback* (*Gasterosteus biaculeatus*). With two spines in front of the dorsal fin.
>
> The smallest of our fishes, scarcely more than an inch in length; and known by the two thorny processes on the back, forward of the dorsal fin. Seems to be the species described by Shaw; and, what is remarkable, the only one that I remember for which he has given credit to the waters of New-York. Caught in the salt water among the killifishes.
>
> 2. *Four-spined Stickleback* (*Gasterosteus quadracus*). . . .

This description is almost worthless; it is made clear, however, that he had a species of three-spined stickleback caught in the salt water of New York along with *Fundulus.* His

[13] Artedi Pisc., 1792: 450.

[14] Zoology, 4, 1803: 608.

[15] Bull. U. S. Nat. Mus., 47, pt. 1, 1896: 748.

[16] Trans. Lit. and Philos. Soc. N. Y., 1815: 430, pl. 1, fig. 10.

name can hardly be treated with Walbaum's and Shaw's as a *nomen nudum*, because his account, especially the statement of habitat, is in fact an indication of identity. It is almost certain that he would have had from this habitat only the local plated form of *Gasterosteus aculeatus*. Mitchill's very crude figure shows little except that he had a three-spined stickleback. The other species mentioned by Mitchill is not congeneric; his *biaculeatus* was obviously intended to designate the common *Gasterosteus* (in the modern generic sense) of New York, which is, significantly, a very frequent associate of the killifishes.

It is virtually sure that Mitchill did not have *Gladiunculus wheatlandi* at hand. That species is not known to occur so far down the coast as New York. The only specimens authentically recorded from south of Cape Cod are young ones secured in open water at Woods Hole. My own collections in the bays about Woods Hole and elsewhere along the south shore of New England, confirming those made there by others, include no examples of *wheatlandi*; it is probable that the killifishes and *Gladiunculus* are virtually complementary in their habitat selection at Woods Hole. No specimens of *wheatlandi* from any locality nearer New York than Woods Hole seem to be known; at least none such are preserved in the National Museum, American Museum, Museum of Comparative Zoology, or the Museum of Zoology.

Richardson[17] confused the accounts of Cuvier and Valenciennes and of Mitchill. De Kay,[18] however, was unable to reconcile the two descriptions; he referred fully plated sticklebacks to *biaculeatus*. Storer[19] then gave a good description and figure of *biaculeatus*, clearly also so designating a race of

[17] Fauna Boreali-Americana, pt. 3, 1836: 56.

[18] New-York Fauna, pt. 4, 1842: 65, pl. 3, fig. 9.

[19] Mem. Amer. Acad. Arts and Sci., 5, 1855: 88, pl. 8, fig. 2, 3 (reprinted as A History of the Fishes of Massachusetts, 1857, with same pagination).

the *aculeatus* series. Girard[20] emphatically stated that Cuvier and Valenciennes had a species distinct from that handled by Mitchill, but he erroneously referred the *biaculeatus* of Cuvier and Valenciennes to the synonymy of his own *cuvieri*, which is clearly the partially armored fresh-water Labrador derivative of *aculeatus*. Disregarding Mitchill's account, Gunther[21] recognized *biaculeatus* on the authority of Cuvier and Valenciennes, and referred Girard's *cuvieri* to the synonymy of *biaculeatus*.

In his terse revision of the genus *Gasterosteus*, Regan[22] passes by *wheatlandi* without mention. In a much more elaborate monograph of the sticklebacks, Bertin[23] recognized not only *wheatlandi* but also *biaculeatus* (in the sense of Cuvier and Valenciennes) and *gladiunculus*. Still less critically, he aligned them all in the *aculeatus* complex. I cannot refrain from stating that Bertin's classification of the sticklebacks appeals to me as a reversion to pre-Darwinian pigeonholing.

To round out the story, it may be mentioned that "*Gasterosteus bispinosus* subsp. *Johanseni*" Cox,[24] recently described from Newfoundland, appears to be synonymous with *wheatlandi*.

Practically all modern American writers, with the exception of Kendall and his followers listed in footnotes 10 and 24, have used the name *biaculeatus* for the local race of *aculeatus*—fully armored and long-spined—which inhabits the shores of the north Atlantic states (Plate I, figure 1).

Unless this local race be recognized as distinct nomenclatorially, I conclude that *biaculeatus* as well as *bispinosus* should be referred to the synonymy of *Gasterosteus aculeatus*.

[20] In Storer, Boston Journ. Nat. Hist., 6, 1857: 254, pl. 7, fig. 1. In this paper Girard recounted the early history of "the two-spined stickleback."

[21] Cat. Fishes Brit. Mus., 1, 1859: 5.

[22] Ann. and Mag. Nat. Hist. (8), 4, 1909: 435–437.

[23] Ann. Inst. Océan. Monaco, 2, 1925: 1–204, 71 figs.

[24] Canadian Field Naturalist, 37, 1923: 146.

The Atlantic American species of three-spined stickleback which is completely differentiated from *aculeatus* should, therefore, no longer be called *biaculeatus*. It should be known as *Gasterosteus wheatlandi* Putnam, or, I think preferably, as *Gladiunculus wheatlandi* (Putnam).

Finally, I wish to thank Dr. Wm. C. Kendall and the United States Bureau of Fisheries, for helpful suggestions and for permission to use the drawings from which the plates illustrating this paper were prepared.

PLATE I

THREE RACES OF GASTEROSTEUS ACULEATUS

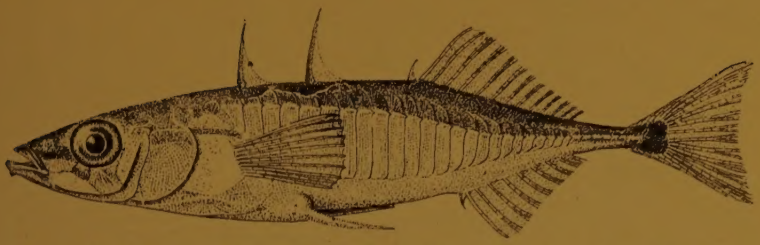

Figure 1. Specimen from Woods Hole, Massachusetts, representing the fully plated, long-spined race of Long Island Sound

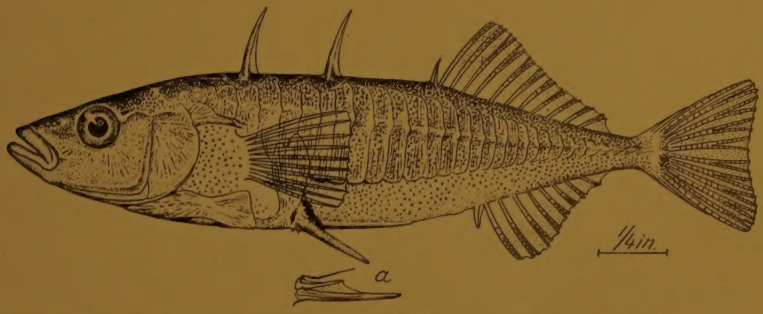

Figure 2. Specimen from Freeport, Maine, representing a less extreme marine type

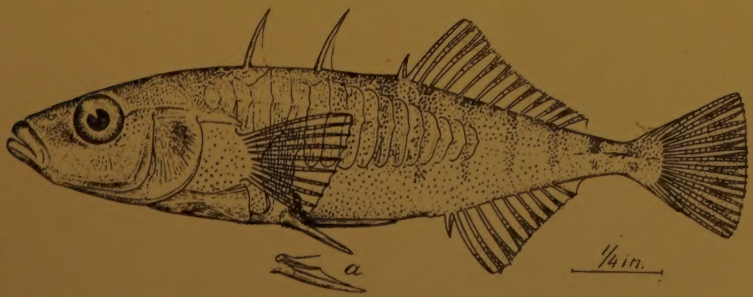

Figure 3. Specimen from Cobbosseecontee Lake, Maine, representing the fresh-water race known as *atkinsii*

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PLATE II

TWO RACES OF GASTEROSTEUS ACULEATUS AND THE SPECIES GLADIUNCULUS WHEATLANDI

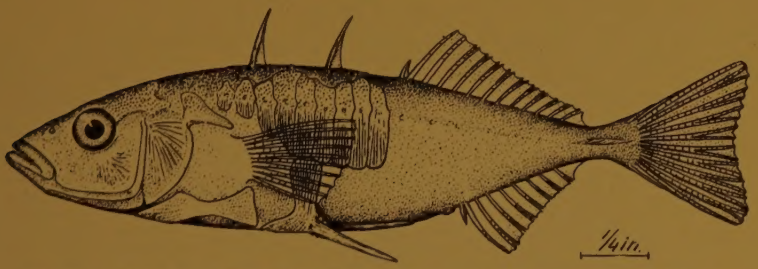

Figure 1. Specimen from "Hudson Bay," representing a moderately extreme fresh-water race of *Gasterosteus aculeatus*

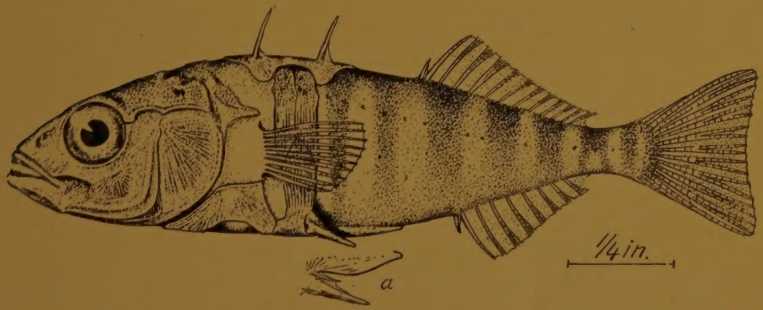

Figure 2. Specimen presumably from southern California, misidentified by Eigenmann as *Gasterosteus wheatlandi*, but really representing *Gasterosteus aculeatus williamsoni*

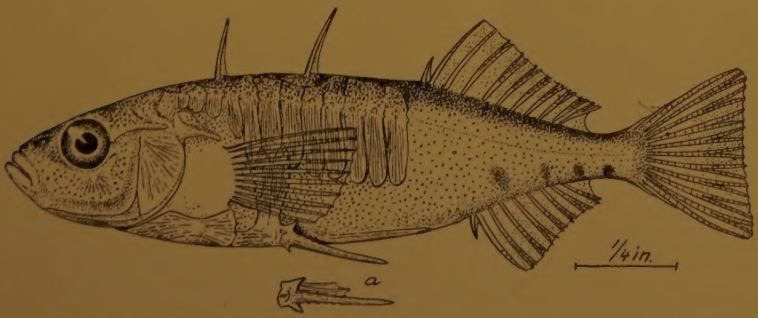

Figure 3. Specimen of *Gladiunculus wheatlandi* from Freeport, Maine, collected by W. C. Kendall.

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